JOURNAL OF MATHEMATICAL ANALYSIS AND APPLICATIONS 62, 157–169 (1978)

Nonlinear Reaction–Diffusion Models for Interacting Populations

STEPHEN A. WILLIAMS* AND PAO-LIU CHOW†

Department of Mathematics, Wayne State University, Detroit, Michigan 48202

Submitted by Alex McNabb

This paper proves that several initial-boundary value problems for a wide class of nonlinear reaction–diffusion equations have solutions $c_i(x, t)$, $1 \leqslant i \leqslant N$ (with $c_i(x, t)$ representing the concentration of the ith species at position x in a set $\bar{\Omega}$ at time $t \geqslant 0$), which exist for all $t \geqslant 0$ and are unique, smooth, nonnegative, and strictly positive for $t > 0$. The Volterra–Lotka predator–prey model with diffusion (to which the results above are proved to apply) is then studied in more detail. It is proved that any bounded solution of this model loses its spatial dependence and behaves like a periodic function of time alone as $t \to \infty$. It is proved that if the spatial dimension is one or if the diffusion coefficients of the two species are equal, then all solutions are bounded.

1. INTRODUCTION

A significant amount of attention has been given to systems of nonlinear reaction–diffusion equations

$$\partial c_i/\partial t = \nu_i \Delta c_i + A_i(c_1, c_2, \ldots, c_N), \qquad 1 \leqslant i \leqslant N \tag{1.1}$$

(see [1–9]). Each unknown function $c_i = c_i(x, t)$ is defined for $t \geqslant 0$ and $x \in \bar{\Omega}$ (Ω is a given open subset of $\mathbb{R}^n$). Each ν_i is a given nonnegative function of (x, t) called the diffusion coefficient. Each A_i is a given function of N variables. In the ith equation, $\nu_i \Delta c_i$ is called the diffusion term and $A_i(c_1, c_2, \ldots, c_N)$ is called the reaction term.

System (1.1) can be used in models describing the multigroup diffusion of neutrons in fissionable matter or the flux of heat and moisture through porous solids [1, p. 134]. It has also been used in several models of nerve conduction [10].

* Research done in part as a visitor at the Courant Institute of Mathematical Sciences, New York University.

† Research partially supported by the U.S. Army Research Office under Grant DAAG 29-76-G-0141.

0022-247X/78/0621-0157$02.00/0

Systems of equations modeling chemical reactions are often of the form (1.1). The set Ω is then the region in which the reactions take place. For $1 \leqslant i < N$, $c_i(x, t)$ represents the concentration at location $x \in \bar{\Omega}$ and time $t \geqslant 0$ of the ith participating molecular species; $c_N(x, t)$ is the temperature at position x and time t [11, p. 265]. (Since $\nu_N \Delta c_N$ models only diffusion of heat, such models are inappropriate unless convection is negligible.) Areas of application for such models include morphogenesis (see [12, pp. 123–126] and [13]) and evolution of biopolymers before the existence of living organisms [14].

The assumptions of the present paper will be those appropriate for still another area in which (1.1) is used: population dynamics. The set Ω is then the region in which N biological species interact, and $c_i(x, t)$ is the concentration of the ith species at position x and time t. The diffusion term $\nu_i \Delta c_i$ models the tendency for net motion of individuals from regions of high concentration to regions of low concentration. The reaction term $A_i(c_1, c_2, \ldots, c_N)$ models the effect on $\partial c_i/\partial t$ of biological interactions such as competition, predation, and symbiosis.

No model of the form (1.1) can be relied on to be in quantitative agreement with real-world biological systems. Volterra, who did most of the early work on such models (without the diffusion terms), already clearly recognized this [15, p. 11]: "Volterra emphasized consistently that differential equations are, at best, only rough approximations of actual ecological systems. They would apply only to animals without age or memory, which eat all the food they encounter and immediately convert it into offspring." System (1.1) can also be criticized as a model because it ignores probabilistic and optimal control aspects of the real-world situation. Nevertheless, system (1.1) is worth studying because it might give better qualitative understanding of certain real-world situations, and because such study might help in constructing and analyzing more complex models.

In this paper we will consider only the case in which

$$A_i(c_1, c_2, \ldots, c_N) = c_i B_i(c_1, c_2, \ldots, c_N), \qquad 1 \leqslant i \leqslant N, \tag{1.2}$$

where each function B_i is given. For models of biological systems, (1.2) is a reasonable assumption (largely because $c_i = 0$ implies $A_i(c_1, c_2, \ldots, c_N) = 0$ for such systems). References [16–18] or [19, p. 69] and [20–23] have considered only systems in which (1.2) holds (they did not consider the effects of diffusion). For models of chemical systems (1.2) is *not* a reasonable assumption in general (clearly $A_i(c_1, c_2, \ldots, c_N) > 0$ can happen even if $c_i = 0$ for such systems).

The main results of this paper are stated in Theorems 1 and 2. Two papers that prove existence and smoothness for systems in situations somewhat similar to that of Theorem 1 are [1] and [24].

The authors are indebted to Professor Avner Friedman for a very helpful discussion.

2. Notation and Definitions

Since the most difficult theorems will be drawn from [25], our notation and definitions will follow that source with only a few stylistic modifications (see [25, pp. 1–10]).

Let δ and ρ_0 be fixed numbers with $0 < \delta < 1$ and $\rho_0 > 0$. If G is an open subset of $\mathbb{R}^n$, $H^{2+\delta}(\bar{G})$ denotes the Banach space of all real-valued functions u continuous on $\bar{G}$ with all first and second order derivatives also continuous on $\bar{G}$ with finite value for the norm

$$| u |_G^{(2+\delta)} = \sum_{0 \leqslant |\alpha| \leqslant 2} \sup_G | D^\alpha u | + \sum_{|\alpha|=2} \sup \frac{|[D^\alpha u](x) - [D^\alpha u](y)|}{| x - y |^\delta},$$

where $\alpha = (\alpha_1, \alpha_2, ..., \alpha_n)$ is a multiindex (an n-vector of nonnegative integers), $| \alpha | = \alpha_1 + \alpha_2 + \cdots + \alpha_n$, $D^\alpha u = \partial^{|\alpha|} u / \partial x_1^{\alpha_1} \partial x_2^{\alpha_2} \cdots \partial x_n^{\alpha_n}$, where each summation is extended over all multiindices satisfying the condition listed beneath it, and where the second supremum is taken over all x and y in $\bar{G}$ such that $0 < | x - y | \leqslant \rho_0$. For each α with $| \alpha | = 2$, this supremum picks out the coefficient of Hölder continuity for $D^\alpha u$ corresponding to Hölder exponent δ.

The "space domain" of this paper is a bounded open subset Ω of $\mathbb{R}^n$ with boundary $\partial\Omega$. We assume that $\partial\Omega \in H^{2+l}$ (where $0 < l < 1$ is fixed throughout this paper), i.e., that there are positive constants ρ and M_1 such that for any $x^0 \in \partial\Omega$ there is a one-to-one map ϕ of the closure of the set $K = \{x = (x_1, x_2, ..., x_n) \in \mathbb{R}^n; x_1^2 + x_2^2 + \cdots + x_{n-1}^2 < 1 \text{ and } | x_n | < 1\}$ into $\mathbb{R}^n$, where $\phi \in H^{2+l}(\bar{K})$, $| \phi |_K^{(2+l)} \leqslant M_1$, $\phi(0, 0, ..., 0) = x^0$, $\phi(\{x_n = 0\} \cap K) = \partial\Omega \cap \phi(K)$, $\phi(\{x_n < 0\} \cap K) = \Omega \cap \phi(K)$, and where $\phi(K)$ contains a ball of radius ρ about x^0. Such a set Ω has a unit outward normal $n = n(x) = (n_1(x), n_2(x), ..., n_n(x))$ at each point x of $\partial\Omega$. The directional derivative in the direction n will be denoted by $\partial/\partial n$. We will say that $\partial\Omega \in C^k$ (for $k \geqslant 1$) if functions ϕ exist as above and are k times continuously differentiable instead of being in $H^{2+l}(\bar{K})$ and having $| \phi |_K^{(2+l)} \leqslant M_1$.

For any $T > 0$, let $Q_T = \Omega \times (0, T)$. For j a nonnegative integer and $0 < \delta < 1$, denote by $H^{j+\delta,(j+\delta)/2}(\bar{Q}_T)$ the Banach space of all real-valued functions u having all derivatives of the form $D^\alpha D_t^r u$ (here α is a multiindex, $r \geqslant 0$ is an integer, and $D_t = \partial/\partial t$) with $2r + | \alpha | \leqslant j$ continuous on $\bar{Q}_T$ and having finite norm

$$\begin{aligned} | u |_{Q_T}^{(j+\delta)} = & \sum_{0 \leqslant 2r+|\alpha| \leqslant j} \sup_{Q_T} | D^\alpha D_t^r u | \\ & + \sum_{2r+|\alpha|=j} \sup \frac{|[D^\alpha D_t^r u](x, t) - [D^\alpha D_t^r u](y, t)|}{| x - y |^\delta} \\ & + \sum_{j-1 \leqslant 2r+|\alpha| \leqslant j} \sup \frac{|[D^\alpha D_t^r u](x, t) - [D^\alpha D_t^r u](x, t')|}{| t - t' |^{(\delta+j-2r-|\alpha|)/2}}, \end{aligned}$$

where the second supremum is extended over all (x, t) and (y, t) in $\bar{Q}_T$ with $0 < | x - y | \leqslant \rho_0$ and where the third supremum is extended over all (x, t) and (x, t') in $\bar{Q}_T$ with $0 < | t - t' | \leqslant \rho_0$. The second and third suprema pick out the coefficients of Hölder continulty for $D^\alpha D_t{}^r u$ with respect to the space and time variables, respectively, with Hölder exponents δ and $(\delta + j - 2r - | \alpha |)/2$, respectively.

3. Results for the General Initial-Boundary Value Problem

THEOREM 1. *Let Ω be a bounded open subset of $\mathbb{R}^n$ with $n \geqslant 1$. Assume that $\partial\Omega \in H^{2+l}$ for some l satisfying $0 < l < 1$. Let $f_1, f_2, \ldots, f_N$ be nonnegative-valued functions in $H^{2+l}(\bar{\Omega})$ whose normal derivatives vanish on $\partial\Omega$. For $1 \leqslant i \leqslant N$ let B_i: $\mathbb{R}^N \to \mathbb{R}$ have continuous partial derivatives up to second order. Let $\nu_1, \nu_2, \ldots, \nu_N$ be given positive constants. Assume the following condition:*

(The food pyramid condition.) For every $M > 0$ and $1 \leqslant i \leqslant N$, there exists a $b_i(M) > 0$ such that $c_1 \geqslant 0$, $c_2 \geqslant 0, \ldots, c_N \geqslant 0$ and $c_1 \leqslant M$, $c_2 \leqslant M, \ldots, c_{i-1} \leqslant M$ imply that $B_i(c_1, c_2, \ldots, c_N) \leqslant b_i(M)$.

Then

(i) *for any constant $T > 0$ the nonlinear parabolic system*

$$\begin{aligned} &\partial c_i/\partial t = \nu_i \Delta c_i + c_i B_i(c_1, c_2, \ldots, c_N) && \text{for } (x, t) \in \bar{\Omega}_T, \quad 1 \leqslant i \leqslant N; \\ &c_i(x, 0) = f_i(x) && \text{for } x \in \bar{\Omega}, \qquad 1 \leqslant i \leqslant N; \\ &(\partial c_i/\partial n)(x, t) = 0 && \text{for } (x, t) \in \partial\Omega \times [0, T], \\ & && \qquad 1 \leqslant i \leqslant N \end{aligned} \tag{3.1}$$

has a solution $(c_1(x, t), c_2(x, t), \ldots, c_N(x, t))$ with $c_i \in H^{2+l,(2+l)/2}(\bar{Q}_T)$ for $1 \leqslant i \leqslant N$. This solution is unique, even among generalized solutions of (3.1);

(ii) *$c_i(x, t) \geqslant 0$ for $(x, t) \in \bar{Q}_T$, $1 \leqslant i \leqslant N$; and*

(iii) *if Ω is connected and no f_i $(1 \leqslant i \leqslant N)$ is identically zero, then each c_i $(1 \leqslant i \leqslant N)$ is strictly positive for $t > 0$.*

Remark 1. The theorem is also true if any or all of the boundary conditions $\partial c_i/\partial n = 0$ are replaced by $c_i(x, t) = \Phi_i(x, t)$ under the conditions of [25, Theorem 5.2, p. 320] with $\Phi_i \geqslant 0$ (in (iii) the conclusion is then that $c_i(x, t) > 0$ for $x \in \Omega$ and $t > 0$). Also, any of the operators $\nu_i \Delta$ can be replaced by more general elliptic operators under the conditions of [25, Theorem 5.3, p. 320]. In particular (perhaps the most important generalization from the point of view of applications), each diffusion constant ν_i can be replaced by a function $\nu_i(x, t)$, Hölder continuous in (x, t) and with $\nu_i(x, t) \geqslant \delta > 0$ (for some constant δ) on each $\bar{Q}_T$. Only slight changes in the proof below are required to establish these statements.

Remark 2. The vast majority of all biological systems have a "food pyramid"; i.e., it is possible to arrange the species in numerical sequence so that if $1 \leqslant i < j \leqslant N$, then the ith species does not use the jth species for food. If $c_1 \leqslant M$, $c_2 \leqslant M, \ldots, c_{i-1} \leqslant M$, then all the species that the ith species might use for food (except the ith species itself) have limited concentrations, so it is reasonable to assume (since cannibalism does not increase the biomass of the ith species) that its growth is limited, i.e., $B_i(c_1, c_2, \ldots, c_N) \leqslant b_i(M)$; note that this allows $c_i(x, t)$ to grow like a constant times $\exp[tb_i(M)]$. The first species in the sequence discussed above (and perhaps a few others) is a primary food producer, not feeding on any other species. Its growth rate is restricted by the limited amount of energy density (e.g., chemical energy in plant species not considered in the system or light energy) in the environment, so it is reasonable to assume that there is a $b_1 > 0$ such that $B_1(c_1, c_2, \ldots, c_N) < b_1$ whenever $c_1 \geqslant 0$, $c_2 \geqslant 0, \ldots, c_N \geqslant 0$. Thus the name of the food pyramid condition is appropriate, and it is reasonable to assume for general biological ecosystems. Symbiosis as well as inter- or intra-species competition or predation are allowed by this assumption.

Remark 3. Note that (iii) implies that, *unlike the situation without diffusion*, no species can be driven to extinction.

Proof of Theorem 1. Let $T > 0$ be fixed. For any positive nonintegral k, let $V(k) = \{(c_1, c_2, \ldots, c_N);\ |c_i|_{Q_T}^{(k)}$ is finite for $1 \leqslant i \leqslant N\}$. Let the norm $\|\cdot\|_{V(k)}$ for $V(k)$ be defined by $\|(c_1, c_2, \ldots, c_N)\|_{V(k)} = |c_1|_{Q_T}^{(k)} + |c_2|_{Q_T}^{(k)} + \cdots + |c_N|_{Q_T}^{(k)}$. A tedious Taylor's theorem argument shows that since each B_i (for $1 \leqslant i \leqslant N$) is twice continuously differentiable, the map $(c_1, c_2, \ldots, c_N) \mapsto B_i(c_1, c_2, \ldots, c_N)$ is from $V(l)$ into $H^{l,l/2}(\bar{Q}_T)$ and is continuous.

For any $(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) \in V(l)$, let $(c_1, c_2, \ldots, c_N)$ be the unique solution in $V(l+2)$ of the problem

$$
\begin{aligned}
&\partial c_i/\partial t = \nu_i \Delta c_i + c_i B_i(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) && \text{for } (x, t) \in Q_T, \quad 1 \leqslant i \leqslant N;\\
&c_i(x, 0) = f_i(x) && \text{for } x \in \bar{\Omega}, \quad 1 \leqslant i \leqslant N;\\
&(\partial c_i/\partial n)(x, t) = 0 && \text{for } (x, t) \in \partial\Omega \times [0, T],\\
& && 1 \leqslant i \leqslant N.
\end{aligned}
$$

This unique solution is guaranteed by applying [25, Theorem 5.3, pp. 320, 321] to the N (separate) initial-boundary value problems for the c_i above. Let $\mathscr{C}: V(l) \to V(l+2)$ be defined by $\mathscr{C}(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) = (c_1, c_2, \ldots, c_N)$. A careful reading of the proof of [25, Theorem 5.3] shows that $\mathscr{C}$ is a continuous map.

Let $\mathscr{I}: V(l+2) \to V(l)$ be the inclusion map; i.e., for every $(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) \in V(l+2)$, $\mathscr{I}(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) = (\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) \in V(l)$. Clearly $\mathscr{I}$ is a bounded linear map. It can also be shown that $\mathscr{I}$ is compact. The map $\mathscr{C}\mathscr{I}: V(l+2) \to V(l+2)$ is therefore compact.

For $1 \leqslant i \leqslant N$, let $a_i = \max\{f_i(x); x \in \bar{\Omega}\}$. We now define numbers $b_1, b_2, \ldots, b_N$ by induction. Let $b_1 > 0$ be the guaranteed constant such that $c_1 \geqslant 0, c_2 \geqslant 0, \ldots, c_N \geqslant 0$ imply that $B_1(c_1, c_2, \ldots, c_N) \leqslant b_1$. Suppose now that $b_1 > 0, b_2 > 0, \ldots, b_{i-1} > 0$ have been chosen (here $1 < i \leqslant N$). Let $M = \max\{a_k e^{b_k T}; 1 \leqslant k < i\}$, and define b_i to be the guaranteed constant such that $c_1 \geqslant 0, c_2 \geqslant 0, \ldots, c_N \geqslant 0$ and $c_1 \leqslant M, c_2 \leqslant M, \ldots, c_{i-1} \leqslant M$ imply that $B_i(c_1, c_2, \ldots, c_N) \leqslant b_i$.

Define $S = \{(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) \in V(l+2); 0 \leqslant \tilde{c}_i(x, t) \leqslant a_i e^{b_i T}$ for $(x, t) \in \bar{Q}_T$ and $1 \leqslant i \leqslant N\}$. Clearly S is a closed convex subset of $V(l+2)$. We will show that $\mathscr{C}\mathscr{I}$ maps S into itself so that the Schauder–Tychonoff fixed point theorem (see, for example, [26, p. 131]) guarantees the existence of a $(c_1, c_2, \ldots, c_N) \in S$ such that $\mathscr{C}\mathscr{I}(c_1, c_2, \ldots, c_N) = (c_1, c_2, \ldots, c_N)$. Obviously $(c_1, c_2, \ldots, c_N)$ is then a solution of (3.1) with $c_i \geqslant 0$ and $c_i \in H^{2+l,(2+l)/2}(\bar{Q}_T)$ for $1 \leqslant i \leqslant N$. Uniqueness even among generalized solutions of (3.1) then follows from [27, pp. 3–7].

It remains to prove (iii) and to show that $\mathscr{C}\mathscr{I}$ maps S into itself; this will be done by several applications of various maximum principles. For $(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) \in S$, let $(c_1, c_2, \ldots, c_N) = \mathscr{C}\mathscr{I}(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N)$ as before. For $1 \leqslant i \leqslant N$ and $(x, t) \in \bar{Q}_T$, define $R_i(x, t) = (c_i(x, t) - a_i e^{b_i t})\, e^{-b_i t}$ and $Q_i(x, t) = -c_i(x, t)\, e^{-Mt}$, where

$$M = \max\{|\, B_i(y_1, y_2, \ldots, y_N)|; 1 \leqslant i \leqslant N, 0 \leqslant y_k \leqslant a_k e^{b_k T} \text{ for } 1 \leqslant k \leqslant N\}.$$

Fix i with $1 \leqslant i \leqslant N$. Since $Q_i(x, 0) \leqslant 0$ for all $x \in \bar{\Omega}$, since $(\partial Q_i/\partial n)(x, t) = 0$ for all $(x, t) \in \partial\Omega \times [0, T]$, since $\partial Q_i/\partial t - \nu_i \Delta Q_i + [-B_i(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) + M] Q_i = 0$ for $(x, t) \in Q_T$, and since $[-B_i(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) + M] \geqslant 0$ we have (by [28, Theorem 7, p. 174], together with the observation that the proof of Theorem 6 can be carried out as before, for $E = Q_T$, if for P of the form (x, T) a sphere through P can be constructed whose interior lies entirely in Q_{T+1} instead of Q_T; $D \cap \{(x, t); t < T\}$ is used instead of the lens shaped region D of Theorem 3, and remark (ii) on p. 169 is applied to the function w of the proof of Theorem 3) that $Q_i(x, t) \leqslant 0$ and thus $c_i(x, t) \geqslant 0$ for all $(x, t) \in \bar{Q}_T$. Moreover, if $c_i(x^0, t_0) = 0$ for some $x^0 \in \bar{\Omega}$ and $t_0 > 0$, then $Q_i(x^0, t_0) = 0$ also, and if Ω is connected we have by [28, Theorem 7, p. 174, and the observation made above] that $Q_i(x, 0) = 0$ for all $x \in \bar{\Omega}$, so that $c_i(x, 0) = f_i(x) = 0$ for all $x \in \bar{\Omega}$. This proves (iii).

Fix i with $1 \leqslant i \leqslant N$. Since $R_i(x, 0) \leqslant 0$ for all $x \in \bar{\Omega}$, since $(\partial R_i/\partial n)(x, t) = 0$ for all $(x, t) \in \partial\Omega \times [0, T]$, and since $\partial R_i/\partial t - \nu_i \Delta R_i = c_i[B_i(\tilde{c}_1, \tilde{c}_2, \ldots, \tilde{c}_N) - b_i]\, e^{-b_i t} \leqslant 0$, we have by [28, Theorems 5 and 6, pp. 173, 174, and the observation made above] that $R_i(x, t) \leqslant 0$ and thus $c_i(x, t) \leqslant a_i e^{b_i t} \leqslant a_i e^{b_i T}$ for $(x, t) \in \bar{Q}_T$. Thus $\mathscr{C}\mathscr{I}$ maps S into itself, so the proof of Theorem 1 is complete.

4. Results for the Volterra–Lotka Predator–Prey Model with Diffusion

The Volterra–Lotka predator–prey model with diffusion is

$$
\begin{aligned}
&\left.\begin{aligned}\partial\phi_1/\partial t &= \nu_1\Delta\phi_1 + (\alpha - \phi_2)\,\phi_1\\ \partial\phi_2/\partial t &= \nu_2\Delta\phi_2 + (\phi_1 - \beta)\,\phi_2\end{aligned}\right\} &&\text{for } (x, t) \in \bar{\Omega} \times [0, \infty),\\
&\phi_1(x, 0) = f_1(x) \qquad \text{and} \qquad \phi_2(x, 0) = f_2(x) &&\text{for } x \in \bar{\Omega},\\
&(\partial\phi_1/\partial n)\,(x, t) = (\partial\phi_2/\partial n)\,(x, t) = 0 &&\text{for } (x, t) \in \partial\Omega \times [0, \infty).
\end{aligned}
\tag{4.1}
$$

Note that there is no loss of generality in assuming that the nonlinear terms of (4.1) are $-\phi_2\phi_1$ and $\phi_1\phi_2$ instead of $-\delta\phi_2\phi_1$ and $\gamma\phi_1\phi_2$ (where δ and γ are positive constants); the change of variables $\Phi_1 = \gamma\phi_1$, $\Phi_2 = \delta\phi_2$ reduces the latter case to the former. In (4.1), ϕ_1 and ϕ_2 represent the concentrations of the prey and predator species, respectively.

If $\phi_1(x, t)$ and $\phi_2(x, t)$ are unique solutions of (4.1), define

$$\tilde{\Phi}_i(t) = \frac{1}{m(\Omega)} \int_\Omega \phi_i(x, t)\, dx$$

for $i = 1, 2$ and $t \geqslant 0$ (here $m(\Omega)$ denotes the Lebesgue measure of Ω).

The period of a periodic solution $(\Phi_1(t), \Phi_2(t))$ of the system of ordinary differential equations

$$\frac{d\Phi_1}{dt} = (\alpha - \Phi_2)\,\Phi_1\,, \qquad \frac{d\Phi_2}{dt} = (\Phi_1 - \beta)\,\Phi_2\,, \qquad -\infty < t < \infty, \tag{4.2}$$

is the time between successive crossings by $(\Phi_1(t), \Phi_2(t))$ of the ray $\{(x, y) \in \mathbb{R}^2;\ x = \beta, y \leqslant \alpha\}$ in tne phase plane. We define the *pseudoperiod* of $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ to be the time between successive crossings by $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ of this same ray (this time may vary as $t \to \infty$).

Theorem 2. *Let Ω be a bounded open subset of $\mathbb{R}^n$ with $n \geqslant 1$. Assume that $\partial\Omega \in C^3$. Let f_1 and f_2 be given nonnegative-valued functions in $H^{2+l}(\bar{\Omega})$ (for some l with $0 < l < 1$) whose normal derivatives vanish on $\partial\Omega$. Assume that Ω is connected and that neither f_1 nor f_2 vanishes identically. Let ν_1, ν_2, α, and β be positive constants.*

Then:

(i) *$\phi_1(x, t)$ and $\phi_2(x, t)$ are infinitely differentiable on $\Omega \times (0, \infty)$.*

(ii) *If there is a positive constant M such that $|\phi_1(x, t)| \leqslant M$ and $|\phi_2(x, t)| \leqslant M$ for all $(x, t) \in \bar{\Omega} \times [0, \infty)$, then $\phi_1(x, t) \to \tilde{\Phi}_1(t)$ and $\phi_2(x, t) \to \tilde{\Phi}_2(t)$ as $t \to \infty$, uniformly for all $x \in \bar{\Omega}$. For every $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ is an ϵ-approximate solution for $t \geqslant T_\epsilon$ of (4.2). There is a* *periodic solution* $(\Phi_1(t), \Phi_2(t))$ *of* (4.2) *whose orbit set* $\{(\Phi_1(t), \Phi_2(t)); -\infty < t < \infty\}$ *is approached as closely as desired by* $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ *for sufficiently large* t. *If* $(\Phi_1(t), \Phi_2(t))$ *is not the equilibrium solution* (β, α), *then the pseudoperiod of* $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ *exists and approaches the period of* $(\Phi_1(t), \Phi_2(t))$ *as closely as desired as* $t \to \infty$.

(iii) *If* $\nu_1 = \nu_2$ *or if* $n = 1$, *then there is a constant* M *as required above.*

Proof. Clearly Theorem 1 (including part (iii)) applies to (4.1) under the assumptions of Theorem 2. The food pyramid condition is easy to check: $\phi_1 \geqslant 0$ and $\phi_2 \geqslant 0$ imply $\alpha - \phi_2 \leqslant \alpha$; $\phi_1 \geqslant 0$ and $\phi_2 \geqslant 0$ together with $\phi_1 \leqslant M$ imply $\phi_1 - \beta \leqslant M$.

Part (i) of Theorem 2 follows by repeated application of [29, Theorem 11, p. 74] to any bounded domain D whose closure is contained in $\Omega \times (0, \infty)$. The hypotheses for the starting values $(p, q) = (2, 1)$ are guaranteed by Theorem 1.

For $x > 0$ and $y > 0$, define $E(x, y) = [\alpha\beta]^{-1}\{x - \beta - \beta \ln(\beta^{-1}x) + y - \alpha - \alpha \ln(\alpha^{-1}y)\}$. For $t > 0$ (so that we have $\phi_1(x, t) > 0$ and $\phi_2(x, t) > 0$) define

$$V_t[\phi_1, \phi_2] = \int_\Omega E(\phi_1(x, t), \phi_2(x, t))\, dx.$$

For $t > 0$ we have, by differentiation under the integral sign, by the chain rule, by use of (4.1) and the definition of E, and by the divergence theorem that

$$\frac{d}{dt}\{V_t[\phi_1, \phi_2]\} = -\frac{\nu_1}{\alpha}\int_\Omega \sum_{k=1}^n \frac{1}{(\phi_1)^2}\left(\frac{\partial \phi_1}{\partial x_k}\right)^2 dx$$

$$-\frac{\nu_2}{\beta}\int_\Omega \sum_{k=1}^n \frac{1}{(\phi_2)^2}\left(\frac{\partial \phi_2}{\partial x_k}\right)^2 dx.$$

Thus for $\lambda = \min(\nu_1/\alpha, \nu_2/\beta)$ and for $t > 0$,

$$\frac{d}{dt}\{V_t[\phi_1, \phi_2]\} \leqslant -\lambda \int_\Omega |\nabla \ln \phi_1|^2 + |\nabla \ln \phi_2|^2\, dx. \tag{4.3}$$

Thus $V_t[\phi_1, \phi_2]$ is a nonincreasing function of t for $t > 0$. Note that $E(x, y) \geqslant E(\beta, \alpha) = 0$ for all $x > 0$ and $y > 0$. Therefore $V_t[\phi_1, \phi_2] \geqslant 0$ for all $t > 0$.

Assume now that there is a positive constant M such that $|\phi_1(x, t)| \leqslant M$ and $|\phi_2(x, t)| \leqslant M$ for all $(x, t) \in \bar{\Omega} \times [0, \infty)$.

Let D be an open set with $\bar{D} \subseteq \Omega$ and $\partial D \in C^2$. Differentiating under the integral sign, using the divergence theorem, and using (4.1) we have for $i = 1, 2$ and $t \geqslant 0$ that

$$\frac{d}{dt}\int_D \sum_{k=1}^n \left(\frac{\partial \phi_i}{\partial x_k}\right)^2 dx = \int_{\partial D} 2\frac{\partial \phi_i}{\partial n}\frac{\partial \phi_i}{\partial t}\, d\sigma(x) - \int_D 2\Delta\phi_i[\nu_i \Delta\phi_i + n_i]\, dx, \tag{4.4}$$

where $n_1 = (\alpha - \phi_2)\phi_1$ and $n_2 = (\phi_1 - \beta)\phi_2$. Taking the limit as D expands to fill up Ω in such a way that the outer unit normals for D converge to those of Ω, by the uniform convergence to a continuous limit of the right-hand side of (4.4) (on bounded t-intervals) we have for $i = 1, 2$ and $t \geqslant 0$ that

$$\frac{d}{dt}\int_\Omega \sum_{k=1}^{n} \left(\frac{\partial \phi_i}{\partial x_k}\right)^2 dx = -2\int_\Omega \Delta\phi_i[\nu_i \Delta\phi_i + n_i]\,dx. \tag{4.5}$$

Since $|\phi_i| \leqslant M$ for $i = 1, 2$, we have $|n_i| \leqslant M(M + \alpha + \beta)$ for $i = 1, 2$. Note that if $\Delta\phi_i[\nu_i\Delta\phi_i + n_i] < 0$ at a point (x, t) we must have $\nu_i |\Delta\phi_i| < |n_i| \leqslant M(M + \alpha + \beta)$ there so that $|\Delta\phi_i| \leqslant \nu_i^{-1}M(M + \alpha + \beta)$. Thus for $i = 1, 2$ and $t \geqslant 0$,

$$\frac{d}{dt}\int_\Omega \sum_{k=1}^{n} \left(\frac{\partial \phi_i}{\partial x_k}\right)^2 dx \leqslant c, \tag{4.6}$$

where $c = 2m(\Omega)\,[(\max\{\nu_1^{-1}, \nu_2^{-1}\})\,M(M + \alpha + \beta)]\,[2M(M + \alpha + \beta)]$.

With $|\phi_1| \leqslant M$ and $|\phi_2| \leqslant M$ we can rewrite (4.3) in the form

$$\frac{d}{dt}\{V_t[\phi_1, \phi_2]\} \leqslant \frac{-\lambda}{M^2}\int_\Omega |\nabla\phi_1|^2 + |\nabla\phi_2|^2\,dx \qquad \text{for } t > 0. \tag{4.7}$$

We claim now that $\int_\Omega |\nabla\phi_1|^2 + |\nabla\phi_2|^2\,dx$ goes to zero as $t \to \infty$. Otherwise there would exist an $\epsilon > 0$ and a sequence $\{t_k;\, k = 1, 2,...\}$ with $t_1 \geqslant 2$ and $t_{k+1} \geqslant 1 + t_k$ for $k = 1, 2,...$ such that $\int_\Omega |\nabla\phi_1|^2 + |\nabla\phi_2|^2\,dx \geqslant \epsilon$ for every t_k in the sequence. Let $\eta = \min\{1, \epsilon/(4c)\}$. In view of (4.6), we have $\int_\Omega |\nabla\phi_1|^2 + |\nabla\phi_2|^2\,dx \geqslant \epsilon/2$ for $t_k - \eta \leqslant t \leqslant t_k$ and $k = 1, 2,....$ Thus from (4.7) we have

$$V_{t_k}[\phi_1, \phi_2] - V_{t_k-\eta}[\phi_1, \phi_2] = \int_{t_k-\eta}^{t_k} \frac{d}{dt}\{V_t[\phi_1, \phi_2]\}\,dt \leqslant \frac{-\lambda}{M^2}\,\frac{\epsilon}{2}\,\eta$$

for $k = 1, 2,....$ Thus $V_t[\phi_1, \phi_2]$ decreases by at least $\lambda\epsilon\eta/(2M^2)$ an infinite number of times as $t \to \infty$, contradicting the fact that $V_t[\phi_1, \phi_2] \geqslant 0$. Thus $\int_\Omega |\nabla\phi_1|^2 + |\nabla\phi_2|^2\,dx \to 0$ as $t \to \infty$ as claimed.

From [30] we have for $i = 1, 2$, $x \in \bar{\Omega}$ and $t > 1$ that

$$\phi_i(x, t) = \int_\Omega u_i(t, x; t - 1, y)\,\phi_i(y, t - 1)\,dy + \int_{t-1}^{t} d\tau \int_\Omega u_i(t, x; \tau, y)\,n_i(y, \tau)\,dy,$$

where $u_i(t, x; s, y)$ is the fundamental solution of $\nu_i\Delta f - \partial f/\partial t = 0$ for the domain

Ω with the boundary condition $\partial f/\partial n = 0$ on $\partial\Omega$. For $1 \leqslant k \leqslant n$, $i = 1, 2$, $x \in \bar{\Omega}$, and $t > 1$ we then have

$$\frac{\partial \phi_i}{\partial x_k}(x, t) = \int_\Omega \frac{\partial u_i}{\partial x_k}(t, x; t-1, y)\, \phi_i(y, t-1)\, dy + \int_{t-1}^{t} d\tau \int_\Omega \frac{\partial u_i}{\partial x_k}(t, x; \tau, y)\, n_i(y, \tau)\, dy.$$

One can obtain the estimate

$$\int_\Omega \left| \frac{\partial u_i}{\partial x_k}(t, x; s, y) \right| dy \leqslant K(t-s)^{-1/2}\, e^{K(t-s)}$$

for $t > s$ and for a suitable constant $K > 0$ by first proving the corresponding estimate for $Z(t, x; s, y)$ by direct computation and then using [30, (3.11) and (3.12), p. 307] together with [31, (3.3), p. 85]. (Compare this estimate with [30, (3.13), p. 307].) Using our estimate together with the bounds $|\phi_i| \leqslant M$ and $|n_i| \leqslant M(M + \alpha + \beta)$, simple estimates show that there is an $\tilde{M}$ such that $|(\partial\phi_i/\partial x_k)(x, t)| \leqslant \tilde{M}$ for $i = 1, 2$, $1 \leqslant k \leqslant n$, $x \in \bar{\Omega}$, and $t > 1$. Since each $\partial\phi_i/\partial x_k$ is continuous on $\bar{\Omega} \times [0, 1]$, we may increase $\tilde{M}$ if necessary so that $|(\partial\phi_i/\partial x_k)(x, t)| \leqslant \tilde{M}$ for $i = 1, 2$, $1 \leqslant k \leqslant n$, $x \in \bar{\Omega}$, and $t \geqslant 0$.

By [32, Lemma 1, p. 370] we have *in case Ω is convex* that for each $(x, t) \in \bar{\Omega} \times [0, \infty)$ and $i = 1, 2$,

$$\left| \phi_i(x, t) - \frac{1}{m(\Omega)} \int_\Omega \phi_i(y, t)\, dy \right| \leqslant \sum_{k=1}^{n} \frac{\delta^n}{nm(\Omega)} \int_\Omega \frac{1}{|x-y|^{n-1}} \left| \frac{\partial \phi_i}{\partial y_k}(y, t) \right| dy, \tag{4.8}$$

where δ is the diameter of Ω. Pick an integer $q > 2$ so large that, defining p by $p^{-1} + q^{-1} = 1$, we have $p(n-1) < n$. Then the $L_p(\Omega)$ norm of $|x - y|^{1-n}$ is bounded so that Hölder's inequality applied to (4.8) gives

$$\left| \phi_i(x, t) - \frac{1}{m(\Omega)} \int_\Omega \phi_i(y, t)\, dy \right| \leqslant \kappa\left(\max_{1 \leqslant k \leqslant n} \| \partial\phi_i/\partial x_k \|_q \right), \tag{4.9}$$

for $i = 1, 2$ and all $(x, t) \in \bar{\Omega} \times [0, \infty)$, where κ is a constant independent of t, and where $\|\cdot\|_q$ denotes the norm in $L_q(\Omega)$. Using the ideas of [32, Remark 4 and Theorem 2, pp. 376, 377], (4.9) can be extended so as to be valid not only for convex Ω, but also for any Ω satisfying the hypotheses of Theorem 2.

Since $q > 2$ and $|\partial\phi_i/\partial x_k| \leqslant \tilde{M}$, we have $\|\partial\phi_i/\partial x_k\|_q \leqslant \tilde{M}^{1-2/q}[\|\partial\phi_i/\partial x_k\|_2]^{2/q}$. We have already proved that $\|\partial\phi_i/\partial x_k\|_2 \to 0$ as $t \to \infty$ for $i = 1, 2$, $1 \leqslant k \leqslant n$. Thus $\|\partial\phi_i/\partial x_k\|_q \to 0$ as $t \to \infty$ also, and therefore by (4.9) we have that $\phi_i(x, t) \to \bar{\Phi}_i(t)$ as $t \to \infty$ for $i = 1, 2$, uniformly for $x \in \bar{\Omega}$.

Since $V_t[\phi_1, \phi_2]$ is nonincreasing and nonnegative, there is a constant $V_\infty \geqslant 0$ such that $V_t[\phi_1, \phi_2] \to V_\infty$ as $t \to \infty$. In the phase plane for the system (4.2), for every $V \geqslant 0$, define $S(V) = \{(x, y); x > 0, y > 0, E(x, y) = V/m(\Omega)\}$. We will consider only the case $V_\infty > 0$ (the case $V_\infty = 0$ is much simpler). Let $\epsilon_0 > 0$ be chosen so that $5\epsilon_0$ is less than both the distance from $S(V_\infty)$ to the coordinate axes and the distance from $S(V_\infty)$ to the point (β, α). For any ϵ with $0 < \epsilon < \epsilon_0$ there is a $\delta > 0$ such that

$$R_\delta = \{(x, y); x > 0, y > 0, V_\infty/m(\Omega) \leqslant E(x, y) \leqslant (V_\infty + \delta)/m(\Omega)\}$$

is contained in an ϵ-neighborhood of the set $S(V_\infty)$. There is a $U_\epsilon > 0$ such that $|\phi_i(x, t) - \tilde{\Phi}_i(t)| \leqslant \epsilon$ for $t \geqslant U_\epsilon$, $x \in \bar{\Omega}$, and $i = 1, 2$, while also $V_\infty \leqslant V_t[\phi_1, \phi_2] \leqslant V_\infty + \delta$ for $t \geqslant U_\epsilon$. For every $t \geqslant U_\epsilon$ the mean-value theorem for integrals assures us that some point of $\{(\phi_1(x, t), \phi_2(x, t)); x \in \bar{\Omega}\}$ must be in R_δ. Then clearly $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ is closer that 3ϵ to $S(V_\infty)$ so that every point of $\{(\phi_1(x, t), \phi_2(x, t)); x \in \bar{\Omega}\}$ is closer than 5ϵ to $S(V_\infty)$. Thus we have shown that the distance from $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ to the set $S(V_\infty)$ goes to zero as $t \to \infty$. Clearly $S(V_\infty)$ is an orbit set of the system (4.2).

We have for $t > 0$ that

$$\frac{d}{dt}\tilde{\Phi}_1 = (\alpha - \tilde{\Phi}_2)\tilde{\Phi}_1 + E_1 \qquad \text{and} \qquad \frac{d}{dt}\tilde{\Phi}_2 = (\tilde{\Phi}_1 - \beta)\tilde{\Phi}_2 + E_2,$$

where

$$E_1 = [m(\Omega)]^{-1}\int_\Omega (\tilde{\Phi}_2 - \phi_2)\phi_1\, dx \qquad \text{and} \qquad E_2 = [m(\Omega)]^{-1}\int_\Omega (\phi_1 - \tilde{\Phi}_1)\phi_2\, dx.$$

Since E_1 and E_2 can be made as small as desired by taking t sufficiently large, it is clear that for every $\epsilon > 0$ there exists a $T_\epsilon > 0$ such that $(\tilde{\Phi}_1(t), \tilde{\Phi}_2(t))$ is an ϵ-approximate solution for $t \geqslant T_\epsilon$ of the system (4.2). The statement about the pseudoperiod is then also clear. This completes the proof of (ii).

To prove (iii), first assume that $\nu_1 = \nu_2 = \nu$. By explicit calculation,

$$\nu\Delta[E(\phi_1, \phi_2)] - \frac{\partial}{\partial t}[E(\phi_1, \phi_2)] = \nu\sum_{k=1}^{n}\left[\frac{1}{\alpha(\phi_1)^2}\left(\frac{\partial\phi_1}{\partial x_k}\right)^2 + \frac{1}{\beta(\phi_2)^2}\left(\frac{\partial\phi_2}{\partial x_k}\right)^2\right] \geqslant 0,$$

while also $(\partial/\partial n)[E(\phi_1, \phi_2)] = 0$, so that for any constant $t_0 > 0$, [28, Theorems 5 and 6, pp. 173, 174] show that for all $(x, t) \in \bar{\Omega} \times [t_0, \infty)$ we have $E(\phi_1(x, t), \phi_2(x, t)) \leqslant \max\{E(\phi_1(y, t_0), \phi_2(y, t_0)); y \in \bar{\Omega}\} < \infty$. Since ϕ_1 and ϕ_2 are bounded for $t \in [0, t_0]$, this proves that there exists a constant M such that $|\phi_1| \leqslant M$ and $|\phi_2| \leqslant M$ for all $(x, t) \in \bar{\Omega} \times [0, \infty)$, if $\nu_1 = \nu_2 = \nu$.

To complete the proof of (iii), make the alternate assumption that $n = 1$. Then Ω is some interval (a, b), where $b > a$. It is easy to see that there is a constant $K > 0$ such that

$$\left|f(\xi) - \frac{1}{b-a}\int_a^b f(\eta)\, d\eta\right| \leqslant K\left[\int_a^b \left(\frac{df}{d\eta}\right)^2 d\eta\right]^{1/2} \qquad (4.10)$$

for all $\xi \in [a, b]$ and all continuously differentiable functions f on $[a, b]$. Pick any constant $t_0 > 0$. Because of (4.3), every time interval of length 1 in $[t_0, \infty)$ must contain a point t^* for which

$$\int_\Omega |\nabla \ln \phi_1(x, t^*)|^2 + |\nabla \ln \phi_2(x, t^*)|^2 \, dx \leqslant \frac{(V_{t_0} - V_\infty + 1)}{\lambda}, \tag{4.11}$$

so that (4.10) gives, with $f(x) = \ln \phi_i(x, t^*)$ and $i = 1, 2$, and upper bound independent of t^* for $|\ln \phi_i(x, t^*) - [b - a]^{-1} \int_a^b \ln \phi_i(y, t^*) \, dy|$. Since $V_t[\phi_1, \phi_2]$ is decreasing and nonnegative, it is bounded; from this fact it is easy to get bounds for $|[b - a]^{-1} \int_a^b \ln \phi_i(y, t^*) \, dy|$. Thus $|\ln \phi_i(x, t^*)|$ and hence $\phi_i(x, t^*)$ can be bounded for all $x \in \bar{\Omega}$ and all t^*. The fact that every interval of length 1 in $[t_0, \infty)$ contains a t^* together with the crude exponential growth estimate $\phi_1(x, t) \leqslant \max\{\phi_1(y, t^*); y \in \bar{\Omega}\} e^{\alpha(t - t^*)}$ for all $x \in \bar{\Omega}$ and $t \geqslant t^*$ (which we saw implicitly in the proof of Theorem 1) then shows that $\phi_1(x, t)$ is bounded for all $(x, t) \in \bar{\Omega} \times [0, \infty)$. Using this bound for ϕ_1 we get an exponential growth estimate for ϕ_2 and thus a bound for $\phi_2(x, t)$ valid for all $(x, t) \in \bar{\Omega} \times [0, \infty)$.

References

1. A. McNabb, Comparison and existence theorems for multicomponent diffusion systems, *J. Math. Anal. Appl.* **3** (1961), 133–144.
2. P.-L. Chow and W. C. Tam, Periodic and traveling wave solutions to Volterra–Lotka equation with diffusion, *Bulletin Math. Biol.* **38** (1976), 643–658.
3. K. P. Hadeler, U. an der Heiden, and F. Rothe, Nonhomogeneous spatial distributions of populations, *J. Math. Biol.* **1** (1974), 165–176.
4. E. W. Montroll, Lectures on nonlinear rate equations, especially those with quadratic nonlinearities, *in* "Lectures in Theoretical Physics," Vol. XA, pp. 531–573, Gordon and Breach, New York, 1967.
5. G. Rosen, Solutions to systems of nonlinear reaction–diffusion equations, *Bull. Math. Biol.* **37** (1975), 277–289.
6. G. Nicolis and J. Portnow, Chemical oscillations, *Chem. Rev.* **73** (1973), 365–384.
7. V. Hlaváček, J. Sinkule, and M. Kubíček, A method for determining effects of diffusion on autocatalytic chemical reactions, *J. Theor. Biol.* **36** (1972), 283–290.
8. G. Rosen, First-order diffusive effects in nonlinear rate processes, *Phys. Lett. A* **43** (1973), 450.
9. H. A. Schwarz, Applications of the spur diffusion model to the radiation chemistry of aqueous solutions, *J. Phys. Chem.* **73** (1969), 1928–1937.
10. J. Rinzel, Neutrally stable traveling wave solutions of nerve conduction equations, *J. Math. Biol.* **2** (1975), 205–217.
11. D. H. Sattinger, Six lectures on the transition to instability, *in* "Nonlinear Problems in the Physical Sciences and Biology" (I. Stakgold, D. D. Joseph, and D. H. Sattinger, Eds.), pp. 261–287, Springer-Verlag, New York, 1973.
12. J. Maynard Smith, "Mathematical Ideas in Biology," Cambridge Univ. Press, London/New York, 1968.

13. A. BABLOYANTZ AND J. HIERNAUX, Models for cell differentiation and generation of polarity in diffusion-governed morphogenetic fields, *Bull. Math. Biol.* **37** (1975), 637–657.
14. I. PRIGOGINE, G. NICOLIS, AND A. BABLOYANTZ, Thermodynamics of evolution, *Phys. Today* **25** (1972), No. 11, 23–28 and No. 12, 38–44.
15. F. M. SCUDO, Vito Volterra and theoretical ecology, *Theor. Pop. Biol.* 2 (1971), 1–23.
16. F. J. AYALA, M. E. GILPIN, AND J. G. EHRENFELD, Competition between species: theoretical models and experimental tests, *Theor. Pop. Biol.* **4** (1973), 331–356.
17. J. MAYNARD SMITH, "Models in Ecology," Cambridge Univ. Press, New York/London, 1974.
18. A. N. KOLMOGOROV, *Giorn. Ist. Ital. Attuari* **14** (1936).
19. N. MINORSKI, "Nonlinear Oscillations," Van Nostrand, Princeton, N. J., 1962.
20. P. SAMUELSON, Generalized predator–prey oscillations in ecological and economic equilibrium, *Proc. Nat. Acad. Sci. U.S.A.* **68** (1971), 980–983.
21. W. L. KILMER, On some reasonable constraints in prey–predator mathematics, *J. Theor. Biol.* **36** (1972), 9–22.
22. P. E. WALTMAN, The equations of growth, *Bull. Math. Biophys.* **26** (1964), 39–43.
23. A. RESCIGNO, The struggle for life: II. Three competitors, *Bull. Math. Biophys.* **30** (1968), 291–298.
24. C. V. PAO, Positive solution of a nonlinear diffusion system arising in chemical reactors, *J. Math. Anal. Appl.* **46** (1974), 820–835.
25. O. A. LADYŽENSKAJA, V. A. SOLONNIKOV, AND N. N. URAL'CEVA, "Linear and Quasi-linear Equations of Parabolic Type," Transl. of Math. Monographs, Vol. 23, American Math. Soc., Providence, R.I., 1968.
26. J. CRONIN, "Fixed Points and Topological Degree in Nonlinear Analysis," Amer. Math. Society, Providence, R.I., 1964.
27. A. FRIEDMAN, Remarks on nonlinear parabolic equations, *in* "Proc. of Symposia in Appl. Math.," Vol. XVII, pp. 3–23, American Math. Soc., Providence, R.I., 1965.
28. M. H. PROTTER AND H. F. WEINBERGER, "Maximum Principles in Differential Equations," Prentice–Hall, Englewood Cliffs, N. J., 1967.
29. A. FRIEDMAN, "Partial Differential Equations of Parabolic Type," Prentice–Hall, Englewood Cliffs, N. J., 1964.
30. S. ITÔ, A boundary value problem of partial differential equations of parabolic type, *Duke Math. J.* **24** (1957), 299–312.
31. S. ITÔ, The fundamental solution of the parabolic equation in a differentiable manifold, *Osaka Math. J.* **5** (1953), 75–92.
32. L. V. KANTOROVICH AND G. P. AKILOV, "Functional Analysis in Normed Spaces," Pergamon, New York, 1964.